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Published in:
Palaeontology

DOI:
[10.1111/j.1475-4983.2008.00777.x](https://doi.org/10.1111/j.1475-4983.2008.00777.x)

Publication date:
2008

Document version
Publisher's PDF, also known as Version of record

Citation for published version (APA):
Waterhouse, D., Lindow, B. E. K., Zelenkov, N., & Dyke, G. (2008). Two new parrots (Psittaciformes) from the Lower Eocene Fur Formation of Denmark. *Palaeontology*, 51(3), 575-582. <https://doi.org/10.1111/j.1475-4983.2008.00777.x>

TWO NEW PARROTS (PSITTACIFORMES) FROM THE LOWER EOCENE FUR FORMATION OF DENMARK

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Typescript received 14 December 2006; accepted in revised form 18 April 2007

Abstract: Two new fossil psittaciform birds from the Lower Eocene ‘Mo Clay’ (Fur Formation) of Denmark (c. 54 Ma) are described. An unnamed specimen is assigned to the extinct avian family of stem-group parrots, Pseudasturidae (genus and species *incertae sedis*), while a second (*Mopsitta tanta* gen. et sp. nov.) is the largest fossil parrot yet known. Both specimens are the first fossil records of these birds from Denmark. Although the phylogenetic posi-

tion of *Mopsitta* is unclear (it is classified as family *incertae sedis*), this form is phylogenetically closer to Recent Psittacidae than to other known Palaeogene psittaciforms and may, therefore, represent the oldest known crown-group parrot.

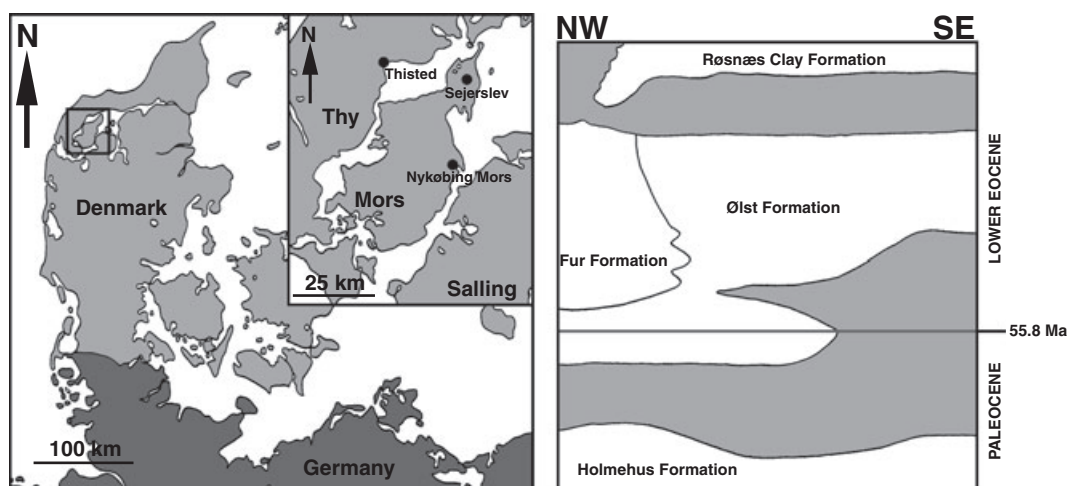
Key words: Aves, Psittaciformes, Pseudasturidae, parrots, Palaeogene, Eocene, Denmark.

PARROTS (Psittaciformes Wagler, 1827) are very familiar birds to us today, being found in most tropical parts of the world. Even though most extant taxa are found in the Southern Hemisphere (Australasia and South America), parrots as a whole range from India to South-East Asia, sub-Saharan Africa and even to North America [the recently extinct Carolina Parakeet *Conuropsis carolinensis* Linnaeus, 1758 (Salvadori 1891) and the Thick-billed Parrot of Mexico, *Rhynchopsitta pachyrhyncha* Swainson, 1827 (Bonaparte 1854)].

No parrots were known from the Palaeogene until about 20 years ago when Harrison (1982) assigned a fossil, *Palaeopsittacus georgei*, from the Lower Eocene London Clay Formation (UK) to the Psittaciformes. However, Mayr and Daniels (1998) suggested that *Palaeopsittacus* was anisodactyl or at best facultatively zygodactyl. Dyke and Cooper (2000) later showed it to be made up of unassociated elements and therefore of uncertain affinity. Subsequently, in the light of new material from Messel, Germany, Mayr (2002a) considered the feet of *Palaeopsittacus* to be preserved in an anisodactyl position, and also remarked on some similarities with Recent Podagraridae (frogmouths). *Quercypsitta sudrei* Mourer-Chauviré, 1992 and *Q. ivani* Mourer-Chauviré, 1992 from the Upper Eocene of Quercy, France, were described as parrots and placed in the new family Quercypsittidae by Mourer-Chauviré (1992). *Psittacopes lepidus* Mayr and Daniels, 1998, com-

prising two nearly complete skeletons from the Middle Eocene of Messel, was assigned to the Psittaciformes. Dyke and Cooper (2000) described *Pulchrapollia gracilis* and also assigned it to this order. Finally, a small (15 mm long) cranial bone fragment from the Cretaceous Lance Formation of Wyoming, USA, was argued by Stidham (1998) to be a crown-group psittaciform, although Dyke and Mayr (1999) considered it to be of uncertain taxonomic affinity because of the fragmentary nature of the material and the possibility that it could be from any number of other taxa, such as a caenagnathid-like theropod dinosaur (Dyke and Mayr 1999; see also Waterhouse 2006).

Pseudasturidae Mayr, 1998 (a family of small Palaeogene zygodactyl birds; Mayr 1998) were originally described as being of uncertain taxonomic affinity. Mayr (2002b) reassigned *Pulchrapollia gracilis* as a pseudasturid (discounting the stout coracoid of the holotype as being from the same taxon as the rest of the material and pointing out similarities between *Pulchrapollia* and pseudasturid specimens held in a private collection from the same Walton-on-the-Naze locality and figured in Mayr 1998 and Mayr and Daniels 1998). In the light of this taxonomic reassignment, he recognised the Pseudasturidae (including *Pulchrapollia* and a number of other Eocene birds) as stem-group Psittaciformes. This placement for *Pulchrapollia* corroborated the original analysis of Dyke and Cooper (2000).



TEXT-FIG. 1. Outline map of Denmark with expanded view of the isle of Mors (the location of the fossil finds) and a simplified north-west–south-east-aligned transect of the Upper Paleocene–lowermost Eocene of the Danish Basin showing the relationship between the Fur Formation (‘Mo clay’) and surrounding sedimentary formations (areas shaded grey indicate hiatuses). Stratigraphy redrawn after Beyer *et al.* (2001, fig. 2); boundary date from Gradstein *et al.* (2004).

Finally, the fossils from the Lower Eocene Fur Formation of Denmark considered in detail herein were briefly mentioned but not formally described and/or positioned taxonomically, as parts of reviews of the ‘Mo Clay’ avifauna by Kristoffersen (2002) and Lindow and Dyke (2006). We describe two new fossil parrots (Psittaciformes) on the basis of this material. One specimen is proposed as a new genus and species of psittaciform, the other as a stem-group psittaciform within the Pseudasturidae.

LOCALITY INFORMATION

As noted above, the two fossils described derive from the Fur Formation (Text-fig. 1) and were collected on the island of Mors by Mr Bent Søren Mikkelsen, the former director of the Møler Museum where the specimens are now housed. Although the Fur Formation is a marine diatomite, classified as a siliceous to clayey siliceous ooze (Pedersen and Surlyk 1983; Pedersen *et al.* 2004), the fossils come from calcareous concretions within the formation, which formed by precipitation of calcite in pore

spaces within the diatomite (Pedersen and Buchardt 1996). Fossil remains within them are preserved in three dimensions because the concretions protected their contents from compaction (Pedersen and Surlyk 1983).

Previously (e.g. Pedersen and Surlyk 1983; Kristoffersen 2002) the formation was considered to be of Paleocene or Paleocene–Eocene age. However, it is now regarded as exclusively Early Eocene (Ypresian) because the Paleocene/Eocene boundary has been identified in the underlying Stolleklint Clay Member of the Ølst Formation (Heilmann-Clausen and Schmitz 2000; Beyer *et al.* 2001; Schmitz *et al.* 2004). This is supported by $^{39}\text{Ar}/^{40}\text{Ar}$ dating of two volcanic ash layers within the Fur Formation, which yielded ages of 54.5 and 54.0 Ma, respectively (Chambers *et al.* 2003).

The Fur Formation is temporally equivalent to the two uppermost members of the Ølst Formation (Beyer *et al.* 2001; Text-fig. 1). On a regional scale, it passes laterally into the clays of the Ølst Formation towards the south and east (Pedersen and Surlyk 1983). Towards the west, it correlates with the offshore Sele and Balder formations of the North Sea Basin (Heilmann-Clausen *et al.* 1985; Pedersen *et al.* 2004).

EXPLANATION OF PLATE 1

Figs 1–4. *Mopsitta tanta* gen. et sp. nov.; FU 110/139, holotype from the Lower Eocene Fur Formation, Denmark; digital photographs of right humerus (coated in ammonium chloride to enhance contrast) in 1, caudal, 2, cranial, 3, right lateral and 4, left lateral views.

Figs 5–8. Pseudasturidae Mayr, 1998 *incertae sedis*, FU 125 from the Lower Eocene Fur Formation, Denmark; digital photographs of left humerus (coated in ammonium chloride to enhance contrast) in 5, caudal, 6, cranial, 7, right lateral and 8, left lateral views.

Scale bars represent 10 mm.



WATERHOUSE *et al.*, *Mopsitta*, *Pseudasturidae incertae sedis*

MATERIAL AND METHODS

Our anatomical terminology follows Baumel and Witmer (1993), but has been simplified in English with reference to Howard (1929); all measurements were made using dial calipers accurate to 0.1 mm and DMW produced all of the line drawings. The phylogenetic diagnoses of the fossils are based on Waterhouse (2005).

Institutional abbreviations. ANMH, American Museum of Natural History, New York, USA; ZMUC CN, Zoological Museum, University of Copenhagen, Denmark; FU, Moler Museum, Mors, Denmark); SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

SYSTEMATIC PALAEOONTOLOGY

Class AVES Linnaeus, 1758
Order PSITTACIFORMES Wagler, 1827
Family *incertae sedis*

Genus MOPSITTA gen. nov.

Derivation of name. After the 'Mo Clay', which is the local designation for the diatomite of the Fur Formation in which the type specimen was discovered, and *Psitta*, a diminutive of the Latin *Psittacus*, a parrot or parakeet.

Type species. *Mopsitta tanta* sp. nov.

Diagnosis. *Mopsitta tanta* was a relatively large psittaciform bird, similar in size to the extant *Cacatua sulphurea* Gmelin, 1788 (Yellow-crested Cockatoo: AMNH 2430, 9040). It can be assigned to Psittaciformes on the basis of: a deep capital groove; pneumatic fossa not expanded distally; cranial margin of humeral head markedly expanded distally in its ventral portion; short deltopectoral crest; well-developed flexor process; wide and deep olecranal fossa.

Mopsitta tanta sp. nov.
Plate 1, figs 1–4; Text-figures 2A, 3A

Derivation of name. Latin, *tantus*, so much, referring to the large size of the holotype specimen when compared with other Eocene Psittaciformes. The type and only specimen was named '*Mopsitta tantus*' in a PhD thesis (Kristoffersen 2002) that remains unpublished; hence this name, with its orthographically incorrect specific epithet, must be regarded as a *nomen nudum*.

Holotype. FU 110/139, a single right humerus, slightly crushed (pieces missing from the shaft, head and deltopectoral crest; Pl. 1, figs 1–4).

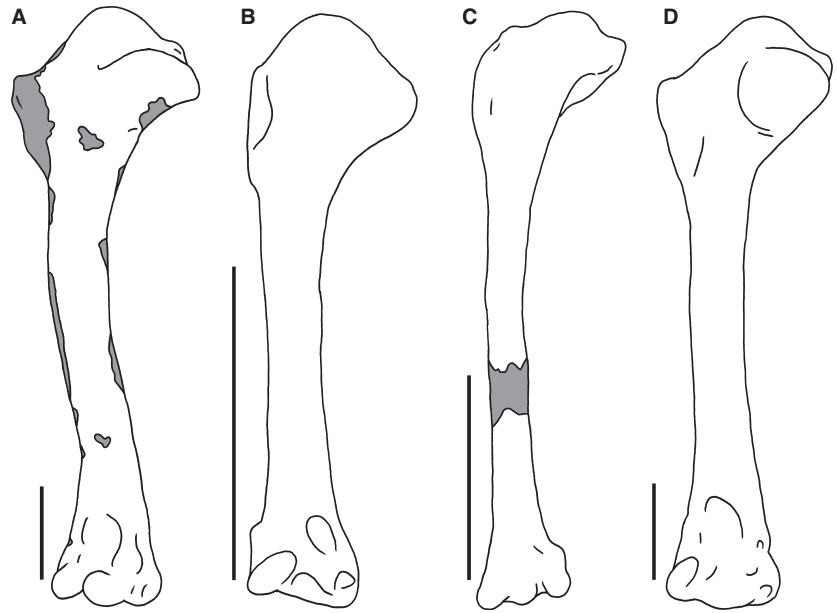
Type horizon and locality. Fur Formation (Text-fig. 1), island of Mors, Jutland, Denmark.

Diagnosis. As for genus.

Description. FU 110/139 is a relatively large, robust bone (Text-fig. 3A); its shaft is strongly bowed and approximately square in cross section (slightly wider than deep, although this is probably because of slight crushing of the bone). A large, well-developed, domed humeral head is present. Most of the deltopectoral crest has broken off, but it is possible to observe that the crest is projected distally; the proximal edge of this crest is situated distal with respect to the humeral head, forming almost a right angle with the long axis of the bone. A relatively small bicipital surface is present, with a concave curve to the distal edge. The wide, shallow bicipital furrow extends to meet the ligamental furrow. The external tuberosity is rounded and extends into the humeral head without a depression in between. The capital groove is deep, wide and open, separated distally from the pneumatic fossa by a thick ridge connected to the internal tuberosity. The pneumatic foramen is a large, deep, rounded, highly pneumatized, pit. The brachial depression is a very shallow excavation. The ectepicondylar prominence and ectepicondyle form a single continuous surface on the lateral margin of the distal humerus. The large, narrow external condyle extends diagonally towards the median of the shaft. The flexor process is well-developed. A small, roughly circular fossa is present laterally, separating the entepicondyle from the entepicondylar prominence. The external tricipital groove is shallower than the internal tricipital groove.

Comparison. *Mopsitta tanta* is distinguished from other Palaeogene psittaciforms that have preserved humeri (i.e. *Psittacopes lepidus* Mayr and Daniels 1998) by its large size, more steeply domed humeral head, more concavely curved bicipital crest, sigmoidally curved shaft, larger brachial depression, more developed internal condyle and entepicondyle, and less prominent entepicondylar prominence (Text-fig. 2B). It differs from other basal Eocene psittaciforms (e.g. the putative pseudasturid '*Primobucco olsoni*' Feduccia and Martin, 1976; Houde and Olson 1989; Mayr and Daniels 1998) by being larger, having a more rounded humeral head, a larger, more rounded bicipital crest, a sigmoidally curved humeral shaft, and a more robust overall shape (Text-fig. 2C). It also differs from Pseudasturidae in having a pneumatic foramen in the pneumatic fossa, poorly developed external tuberosity, a shorter flexor process, and a large external condyle. It differs from extant Psittaciformes (e.g. *Eclectus roratus* Müller, 1776: *Eclectus* Parrot; ZMUC CN 10.6.94) by having a more convex and curved distal edge to the bicipital crest, a more sigmoidally curved shaft (although the shaft is rather strongly curved in *Cacatua*), and a wider external tricipital groove (Kristoffersen 2002) (Text-fig. 2D).

TEXT-FIG. 2. Comparative line drawings. A, right humerus, *Mopsitta tanta* gen. et. sp. nov., FU 110/139 (reconstructed), cranial view. B, left humerus (in mirror image for comparative purposes), *Psittacopes lepidus*, SMF-ME 1279 (redrawn from Mayr and Daniels 1998), cranial view. C, right humerus (in mirror image for comparative purposes), '*Primobucco*' *olsoni* (Pseudasturidae Mayr, 1998), caudal view; private collection (redrawn and reconstructed from Mayr and Daniels 1998: composite drawing from a caudal proximal humerus and a cranial distal humerus), cranial view. D, right humerus, *Eclectus roratus*, ZMUC CN 10.6.94, cranial view. Scale bars represent 10 mm.



The specimen also displays some similarities to the Middle Eocene Ibis *Rhynchaetes messelensis* (Ciconiiformes: Threskornithidae) (Peters 1983). However, anatomically *Mopsitta tanta* is clearly different from Threskornithidae, and thus from *Rhynchaetes*, on the basis of the characters listed in the diagnosis apart from the first and the last. *Mopsitta* can be further distinguished from *Rhynchaetes* by its size (*Rhynchaetes* is considerably smaller), the shape of the capital groove, and because it has a narrower shaft, a more robust median crest and a narrower external tuberosity. The Eocene bird *Palaeopsittacus georgei* Harrison, 1982, of uncertain taxonomic affinity as noted above (see also Dyke and Cooper 2000), has a smaller humerus than that of *Mopsitta*: the humerus of *Palaeopsittacus* was also described by Mayr (2002a) as being long and slender, unlike the more robust humerus of *Mopsitta*; it also seems to be somewhat less sigmoidally curved.

Family PSEUDASTURIDAE Mayr, 1998

Genus and species *incertae sedis*

Plate 1, figures 5–8, Text-figures 3B, 4A

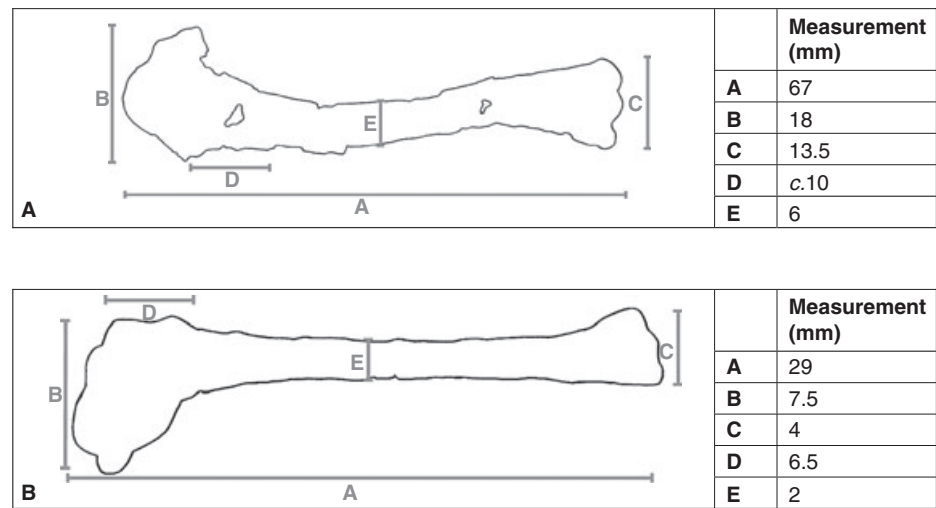
Referred material. FU 125, an almost complete left humerus (some damage to the deltopectoral crest; Pl. 1, figs 5–8).

Diagnosis. Small psittaciform bird, referred to Pseudasturidae Mayr, 1998 on the basis of the following characters: small bicipital crest; external tuberosity

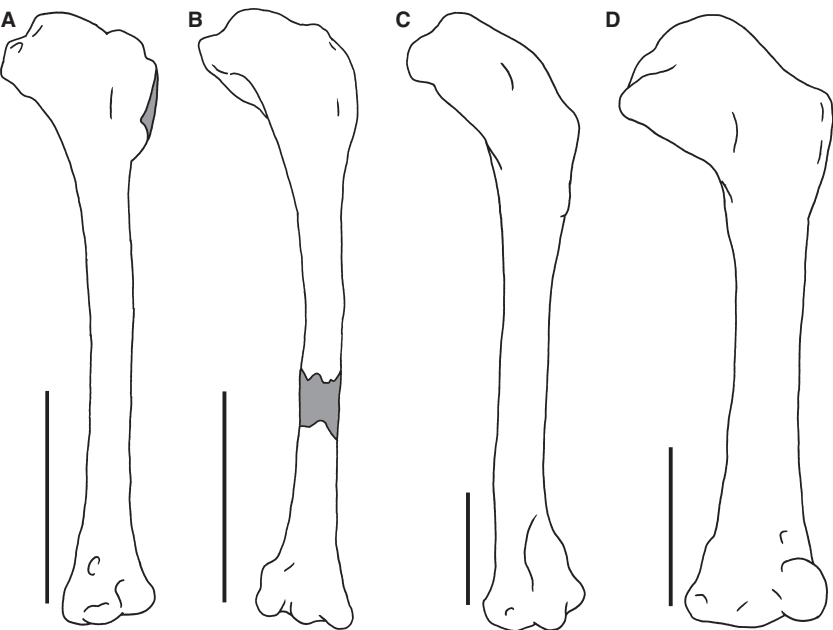
moderately developed; shallow, relatively short ligamental furrow; slender humerus; slightly sigmoidally bowed shaft (in lateral view); small, round internal condyle.

Description. FU 125 is long and slender and has a slightly sigmoidally curved shaft. The shallow ligamental furrow does not extend further laterally than the humeral head. The lateral edge of the deltopectoral crest is broken, but it seems to have a poorly developed external tuberosity. The bicipital crest is relatively small, with a concave curve along its distal edge. The pneumatic foramen is comparatively large and well excavated, with a robust median crest. The capital groove is a relatively small opening on the proximal surface, extending out onto a large, shallow, pneumatic fossa. A slender shaft, circular in cross section with no visible foramen, extends with a slight sigmoidal curve to the distal end of the bone (lateral aspect). Overall, the entire distal end of the humerus is small. A small, but relatively well excavated, triangular internal tricipital groove is also present. The external tricipital groove is smaller in area than the latter but more deeply excavated. An ovoid, shallow, brachial muscle impression is contained within a larger, shallower, brachial depression.

Comparisons. Pseudasturids closely resemble Recent Galbulae in their humeral morphology but have a shorter deltopectoral crest (Mayr 2002b). The taxon described differs from extant psittaciforms, such as *Chalcopsitta atra* Scopoli, 1786 (Black Lory; ZMUC CN 92.206), in being proportionately longer and much more slender, with a smaller deltopectoral crest, a smaller distal end to the humerus with a longer flexor process, and smaller external condyle (Text-fig. 4D).



TEXT-FIG. 3. A–B, measurements of *Mopsitta tanta* gen. et. sp. nov (FU 110/139) and *Pseudasturidae incertae sedis* Mayr, 1998 (FU 125) respectively, with line diagrams to show where these were taken.



TEXT-FIG. 4. Comparative line drawings. A, left humerus, *Pseudasturidae incertae sedis* Mayr, 1998, FU 125, cranial view. B, right humerus ‘*Primobucco*’ *olsoni* (*Pseudasturidae* Mayr, 1998); private collection (redrawn and reconstructed from a caudal proximal humerus and a cranial distal humerus), caudal view. C, left humerus, *Falco vespertinus*, ZMUC CN 92.556, cranial view. D, left humerus, *Chalcopsitta atra*; ZMUC CN 92.206, cranial view. Scale bars represent 10 mm.

DISCUSSION

Mopsitta tanta is in many respects, more similar to Recent Psittaciformes than to any other Palaeogene psittaciform. Although it is not absolutely certain on the basis of preserved features (humeral morphology cannot be entirely diagnostic at this level), it is highly likely that *Mopsitta tanta* is a member of Psittacidae, therefore providing further support to the hypothesis of an early Eocene (or earlier) radiation of Psittaciformes; it is likely that representatives of crown-group Psittaciformes such as *Mopsitta*, existed in the Early Eocene alongside their

stem-group counterparts *Pseudasturidae* and *Quercypsittacidae*.

The remains reported here are the most northerly parrot fossils yet known, as well as the first fossil remains from this clade to be found in Scandinavia. Their discovery (along with other Early Eocene psittaciform remains from Europe) suggests an Early Eocene (or earlier) Old World centre of origin for parrots and their relatives because, so far, no Gondwanan Psittaciformes have been found in sediments younger than Middle Miocene (Boles 1993). However, because early parrot fossils from the New World and Southern Hemisphere have not been

found, a Gondwanan origin cannot be entirely ruled out (see Cracraft 1973, 2001; but also Mayr and Daniels 1998). The timing of the radiation of modern bird groups (Neornithes) remains controversial in evolutionary biology (Dyke and van Tuinen 2004). Many molecular-based studies suggest a Cretaceous origin for modern birds (e.g. Cooper and Penny 1997; van Tuinen and Hedges 2001; Paton *et al.* 2002), whereas fossil discoveries along with some recent molecular studies seem to suggest a post K/T divergence (e.g. Wyles *et al.* 1983; Olson 1985; Feduccia 1995, 2003; Ericson *et al.* 2006). The current restricted molecular data present evidence for a Cretaceous diversification for parrots (Miyaki *et al.* 1998), but the only way to resolve this problem is to find more fossils (Dyke and Cooper 2000). The presence of basal psittaciforms in Northern Europe, along with other, previously described parrots from the Eocene of Europe (e.g. Mourer-Chauviré 1992; Mayr 1998; Mayr and Daniels 1998; Dyke and Cooper 2000), and no real fossil record of parrots below the K/T boundary (Dyke and Mayr 1999) is certainly consistent with an early Cenozoic radiation for (at least) the psittaciforms (Dyke and Cooper 2000).

Acknowledgements. We thank Henrik Madsen and the staff of the Moler Museum for allowing us access to specimens, Bent Søe Mikkelsen for discovering these fossils, and Jon Fjeldså for access to comparative material in Copenhagen. We are also very grateful to Anette Kristoffersen for her suggestion that these specimens were psittaciforms (Kristoffersen 2002), although all descriptions, comparisons, discussions and conclusions in this paper are entirely our own. Jørn Larsen, John O'Brien and Adam Stuart Smith are thanked for their help and/or comments. DMW was funded by a UCD postgraduate scholarship; this project and BEKL are supported by the Irish Research Council for Science, Engineering and Technology (IRCSET). NVZ is supported by grant RFFI 04-04-48829 and the 'Leading Scientific School' (project 1840.2003.4).

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